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A taxonomic review of *Bagarius* catfish (Siluriformes, Sisoridae) in the Salween and Irrawaddy rivers, with descriptions of two new species from China and Myanmar

Yu-Yang Zeng[1,2,3,4], Xin-Rui Pu[5], Hao-Tian Lei[6], Thaung Naing Oo[7], Xiao-Yong Chen[1,2,3]

1 *State Key Laboratory of Genetic Resources and Evolution & Yunnan Key Laboratory of Biodiversity and Ecological Conservation of Gaoligong Mountain, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China*
2 *Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw, Myanmar*
3 *Yunnan International Joint Laboratory of Southeast Asia Biodiversity Conservation, Mengla, China*
4 *University of Chinese Academy of Sciences, Beijing, China*
5 *Yunnan Agriculture University, Kunming, China*
6 *Chinese Agriculture University, Beijing, China*
7 *Department of Forest, Ministry of Natural Resources and Environmental Conservation, Nay Pyi Taw, Myanmar*

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Corresponding author: Xiao-Yong Chen (chenxy@mail.kiz.ac.cn)

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Abstract

The genus *Bagarius* is a group of large, benthic, predatory catfishes found in South and Southeast Asia. Two new species of *Bagarius*, *B. protos* Zeng & Chen, **sp. nov.**, and *B. dolichonema* Zeng & Chen, **sp. nov.**, are described from the Salween River Basin, Yunnan Province, China, and Irrawaddy River Basin, Myanmar, respectively. *Bagarius protos* and *B. dolichonema* both differ from *B. vegrandis* and *B. suchus* in their large size and the adipose-fin origin being nearly vertical to the anal-fin origin. *Bagarius protos* most closely resembles *B. lica* and *B. rutilus* in overall morphology but can be distinguished from *B. lica* by the absence of the brow ridge formed by the lateral margin of the frontal and from *B. rutilus* by the dark yellow (instead of orange) coloration of the fins in life. It further differs from two other congeners in its short filamentous extensions of the pectoral-fin spine. *Bagarius dolichonema* is morphologically and genetically most similar to *B. bagarius*; it can be distinguished from *B. bagarius* by strong dorsal spines slightly flattened immediately anterior to the adipose fin, distally slender neural spines of the 4th–6th vertebrae, and shorter filamentous extensions of the pectoral-fin spine. This new species further differs from three other congeners by its longer filamentous extensions of the pectoral-fin spine and weak notches in the anterodorsal margin of the first dorsal pterygiophores. Molecular phylogeny based on the cytochrome c oxidase subunit I (*CO*I) gene also confirms the validity of these two new species. The estimated K2P genetic distances between *B. protos* and congenerics range from 8.0% to 12.6%, and between *B. dolichonema* and congenerics range from 5.7% to 12.1%.

Key Words

Cryptic species, phylogeny, Southeast Asia, taxonomy

Introduction

The genus *Bagarius* is a group of large predatory fish and includes some of the largest catfishes in Asia, known for its large size and odd appearance. The largest individuals can reach lengths of up to 2 m (Allan et al. 2005), while the smallest, *Bagarius vegrandis* Ng & Kottelat, 2021, still exceed 20 cm in standard length. Jiang et al. (2019a, 2019b) obtained the whole genome sequence of *B. lica* and explored the genetic basis for the species' remarkable size. In contrast to the enormous size of these catfish, their survival is in a deteriorating condition. For example, Sun

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et al. (2023) found that the distribution range of *B. lica* has decreased by 32.8% since 2010, possibly due to the construction of river barriers in the Lancangjiang River. Similarly, Rabbani (2023) found low genetic diversity—indicative of population decline—in *B. bagarius* from the Indus River based on microsatellite DNA analyses.

Bagarius can be distinguished from other sisorid fishes by a series of unique characteristics, including jaw teeth of unequal sizes and a suite of other characters in the neurocranium, splanchnocranium, hyoid apparatus, branchial arches, Weberian apparatus, and latero-sensory system (Ng 2015). *Bagarius* is widely distributed across South and Southeast Asia, with records spanning from the Indian subcontinent to Borneo (Ng and Kottelat 2021). Despite this broad distribution, only five valid species are currently recognized (Roberts 1983; Ng and Kottelat 2000, 2021): *B. bagarius* (Hamilton, 1822), *B. rutilus* Ng & Kottelat, 2000, *B. suchus* Roberts, 1983, *B. lica* Volz, 1903, and *B. vegrandis* Ng & Kottelat, 2021. This low species diversity across such a vast range may indicate an underestimation of the true diversity within the genus. Ng and Kottelat (2021) reassessed the identities of *Bagarius* species from the Indian subcontinent and Southeast Asia, clarified the distributional ranges of *B. bagarius* and *B. lica*, treated *B. yarrelli* as a junior subjective synonym of *B. bagarius*, and suggested that the *Bagarius* populations from the Irrawaddy and Salween rivers may represent two undescribed species. Morphological and molecular phylogenetic studies based on specimens collected in China and Myanmar between 2004 and 2024 support this view and reveal that *Bagarius* from the Salween and Irrawaddy rivers represent two new species, herein named *B. protos* and *B. dolichonema*, respectively. The purpose of this paper is to formally describe these two unnamed species to facilitate a more comprehensive understanding of fish diversity in Southeast Asia.

Materials and methods

Specimens were collected from China and Myanmar between 2004 and 2024. All specimens were initially preserved in 10% formalin and subsequently transferred to 75% ethanol for long-term storage. Some were preserved in analytically pure alcohol, with the right ventral fin clipped for molecular analysis. This preserved tissue was used for phylogenetic analysis. Voucher specimens of *Bagarius protos* and part of *B. dolichonema* are deposited in the Kunming Zoological Museum, Kunming Institute of Zoology (**KIZ**), Chinese Academy of Sciences. The remaining voucher specimens of *B. dolichonema* are deposited at the Southeast Asian Biodiversity Research Institute, Chinese Academy of Sciences, Nay Pyi Taw, Myanmar. In this study, we examined the morphology of specimens of the five recognized species of *Bagarius* for comparative purposes, using material from the Kunming Zoological Museum: *B. suchus*, *B. lica*, *B. rutilus*, *B. bagarius*, and *B. vegrandis*.

Osteological features, vertebral counts, and fin ray counts were assessed using X-ray imaging. Measurements were taken using a micrometer caliper and recorded to the nearest 0.1 mm. Counts and measurements were taken on the left side of each specimen whenever possible. In tables and text, subunits of the head are expressed as proportions of head length (**HL**), and measurements of the head and body are expressed as proportions of standard length (**SL**). Measurements and terminology follow those of Ng and Kottelat (2013), except for caudal-fin length, defined here as the length of the longest ray of the upper lobe measured from the posterior margin of the hypural complex, and dorsal-fin width, defined as the width of the dorsal-fin base.

Fifteen cytochrome c oxidase subunit I (***CO*I**) gene sequences from six *Bagarius* species were obtained and uploaded to NCBI GenBank. An additional ten *CO*I sequences for relevant *Bagarius* species were downloaded from GenBank (Table 1). In total, 25 *CO*I sequences representing seven *Bagarius* species were used in the molecular phylogenetic analysis. *Glyptothorax burmanicus* Prashad & Mukerji was used as the outgroup to represent *Glyptothorax*, the sister group of *Bagarius* (Ng and Jiang 2015). *Pseudecheneis immaculata* Chu was also included as an outgroup.

MEGA 11 (Tamura et al. 2021) was used to align the sequences and calculate genetic distances between species. Both maximum likelihood (ML) and Bayesian inference (BI) methods were used to reconstruct phylogenetic relationships. ML phylogenies were inferred using IQ-TREE (Nguyen et al. 2015) with ultrafast bootstrap support (Minh et al. 2020) based on 1,000 iterations. BI analyses were conducted with MrBayes v3.2.6 (Ronquist et al. 2012) within PhyloSuite v1.2.2 (Zhang et al. 2020). The best-fitting nucleotide substitution models were selected using ModelFinder (Kalyaanamoorthy et al. 2017) based on the Bayesian Information Criterion (BIC): TVM+I+G for ML and HKY+I+G for BI analyses. The BI analysis consisted of two independent runs of Markov Chain Monte Carlo (MCMC), each with one cold and three heated chains, for 10 million generations. Trees were sampled every 1,000 generations, and the first 25% of trees were discarded as burn-in. Convergence was confirmed when the average standard deviation of split frequencies dropped below 0.01. The resulting phylogenetic tree was visualized and edited using FigTree v1.4.4.

Results

Bagarius protos Zeng & Chen, sp. nov.

https://zoobank.org/E27E3A2B-FDBA-4797-84AA-27B93CACC97A

Figs 1, 2, Table 2

Bagarius yarrelli: Chu et al. 1990: 194–195 (Nujiang River, Yunnan, China, in part); Chu 1999: 117–118 (Nujiang River, Yunnan, China, in part); Chen 2013: 319 (Nujiang River, Nantinghe River, Yunnan, China, in part).

Bagarius sp. 'Salween' Ng & Kottelat, 2021:141(Salween River).

Type material. ***Holotype.*** • KIZ2024000178, 319 mm SL; Sanjiangkou [三江口], Salween River [怒江], Longling

Table 1. Collection localities and accession numbers of molecular samples.

	Taxon	Locality	Drainage	Accession number
Ingroup				
(1)	*Bagarius bagarius* 1	Pakistan	Indus River	OP575564
	Bagarius bagarius 2	Andhra, India	Godavari River	OP038550
	Bagarius bagarius 3	West Bengal, India	Ganges River	FJ459434
	Bagarius bagarius 4	Khulna, Bangladesh	Malancha River	MF611596
	Bagarius bagarius 5	Xizang, China	Yarlung Zangbo River	MT812081
(2)	*Bagarius lica* 1	Yunnan, China	Langcangjiang River	PV669786
	Bagarius lica 2	Yunnan, China	Langcangjiang River	PV669787
	Bagarius lica 3	Pahang, Malaysia	Pahang River	HM156380
	Bagarius lica 4	Thailand	unknown	MK448163
(3)	*Bagarius vegrandis* 1	Kanchanaburi, Thailand	Mekong river	OK077104
	Bagarius vegrandis 2	Yunnan, China	Langcangjiang River	PV669800
(4)	*Bagarius rutilus* 1	Yunnan, China	Yuanjiang River	PV669792
	Bagarius rutilus 2	Yunnan, China	Yuanjiang River	PV669797
(5)	*Bagarius suchus* 1	Thailand	unknown	PV669798
	Bagarius suchus 2	Thailand	unknown	PV669799
(6)	*Bagarius protos* sp.nov. 1	Yunnan, China	Nujiang River	PV669788
	Bagarius protos sp.nov. 2	Yunnan, China	Nujiang River	PV669789
	Bagarius protos sp.nov. 3	Yunnan, China	Nujiang River	PV669790
	Bagarius protos sp.nov. 4	Yunnan, China	Nujiang River	KM610422
	Bagarius protos sp.nov. 5	Yunnan, China	Nanting River	PV669791
(7)	*Bagarius dolichonema* sp.nov. 1	Sagaing, Myanmar	Chindwin River	PV669793
	Bagarius dolichonema sp.nov. 2	Sagaing, Myanmar	Chindwin River	PV669794
	Bagarius dolichonema sp.nov. 3	Sagaing, Myanmar	Chindwin River	PV669795
	Bagarius dolichonema sp.nov. 4	Bago, Myanmar	Irrawaddy River	PV669796
	Bagarius dolichonema sp.nov. 5	Manipur, India	Lokchao River	KJ909351
	Outgroup			
(8)	*Glyptothorax burmanicus*	Yunnan, China	Longchuanjiang River	HQ593567
(9)	*Pseudecheneis immaculata*	Yunnan, China	Langcangjiang River	MT5477096

County [龙陵县], Baoshan City [保山市], Yunnan Province [云南省], China, 24°25'05"N, 98°58'31"E; leg. Yu-Yang Zeng, Ling Wu & Cai-Xin Liu, May 2024.

Paratypes. • KIZ2024000179, 1 ex, 372 mm SL, other information same as holotype; • KIZ202400180-181, 2 ex, 391–398 mm SL; Bizhai Township [碧寨乡], Salween River, Longling County, Baoshan City, Yunnan Province, China, 24°27'39"N, 99°00'48"E; leg. Yu-Yang Zeng, Ling Wu, Tao Qin & Jian-Bing Lvy, April 2024; • KIZ2002009301-9302, 2 ex, 393–403 mm SL, Daxueshan Township [大雪山乡], Nanting River [南汀河], Yongde County [永德县], Lincang City [临沧市], Yunnan Province, China, 24°01'02"N, 99°45'23"E, leg. Xiao-Yong Chen, 2002; • KIZ2004015367, 1 ex, 282.6 mm SL, Baihua Village [白花村], Salween River, Longyang District [隆阳区], Baoshan City, Yunnan Province, China, 24°50'05"N, 98°53'50"E leg. Zai-Yun Li, September 2004; • KIZ2004015368, 1 ex, 261.2 mm SL, Hongqiqiao Bridge [红旗桥], Salween River, Longyang District, Baoshan City, Yunnan Province, China, 24°43'58"N, 98°58'16"E, leg. Zai-Yun Li, September 2004; • KIZ2004015372,1 ex, 289.9 mm SL, Sanjiangkou, Salween River, Longling County, Baoshan City, Yunnan Province, China, 24°25'05"N, 98°58'31"E, leg. Zai-Yun Li, September 2004; • KIZ202410548, 1 ex, 324 mm SL, Hehai Village [贺海村], Nanting River [南汀河], Gengma County [耿马县], Lincang City [临沧市], Yunnan Province, China, 23°34'27"N, 99°03'57"E, leg. Yu-yang Zeng, 2024.

Diagnosis. *Bagarius protos* can be distinguished from congeners by having the following combination of characteristics: eye small (5–8% HL), lateral margin of frontal straight, not forming brow ridge, strongly notched in antero-dorsal margin of the first dorsal-fin pterygiophore, dorsal spine strong (width 10.6–14.4 times its length), filamentous extensions of pectoral-fin spine reaching posterior of anal-fin base, neural spines of 4th–6th vertebrae immediately anterior to adipose fin distally slender, adipose-fin origin at vertical through or very slightly posterior to anal-fin origin, caudal peduncle deep (4.2–5.1% SL).

Description. Morphometric data are shown in Table 2. Head depressed, body subcylindrical, slightly compressed laterally at origin of anal fin. Dorsal profile rising uniformly from tip of snout to origin of dorsal fin, body depth at maximum at the origin of the dorsal fin, then sloping gently ventrally from origin of dorsal fin to end of caudal peduncle. Ventral profile flattened to base of anal fin, and then sloping gently dorsally from anal-fin base to caudal-fin base. Anus and urogenital openings located approximately 1/2 to 2/3 distance between end of pelvic-fin base and origin of anal-fin ray. Skin keratinized, with tubercles of various sizes on both sides of body; larger tubercles sparsely placed longitudinally along dorsal surface of head and dorsum. Lateral line complete, situated in midline of body. Vertebrae 23+20 = 43*(4).

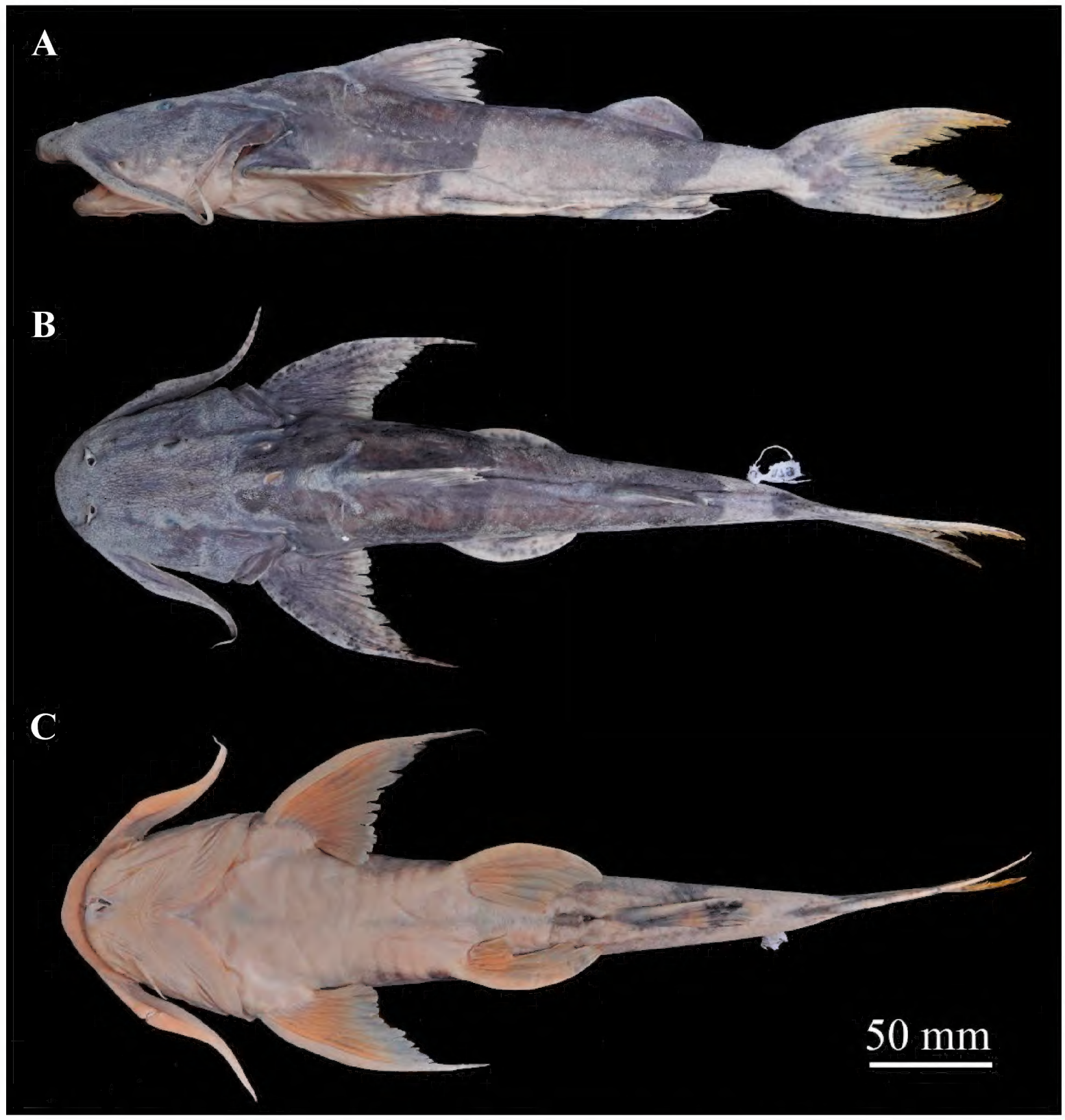

Figure 1. Lateral (**A**), dorsal (**B**), and ventral (**C**) views of *Bagarius protos* sp. nov., KIZ2024000178, holotype, 319 mm SL.

Head depressed and wide. Snout long, about half of head length. Anterior and posterior nares adjacent and separated. Gill opening broad, extending to isthmus. Dorsal surface of head covered by thick skin and ovoid tubercles. Eye small and ovoid; lateral margin of frontal not forming brow ridge.

Barbels in four pairs, including a pair of maxillary barbels, one pair of nasal barbels, and two pairs of mandibular barbels. Maxillary barbel subtended by large skin flap along posterior edge of proximal half of barbel; extending to middle of pectoral-fin base. Nasal barbel short, extending to posterior margin of posterior nares. Outer mandibular barbel extending beyond vertical line through eye. Inner mandibular barbel about 2/3 length of outer mandibular barbel.

Mouth inferior, with premaxillary dental bands partially exposed when mouth closed. Oral teeth cone-shaped, varying in size, and irregularly aligned on all tooth-bearing surfaces. Premaxillary teeth form a broad semilunar band, interrupted at midline.

Dorsal fin located at midpoint of body, with 6 branched fin rays; dorsal spine straight and strong, with smooth anterior and posterior margins, width 10.6–14.4 times its length. Adipose fin triangular, origin at vertical through or very slightly posterior to anal-fin origin. Caudal fin strongly forked, upper lobe longer than lower lobe, with i,7,8,i principal rays. Anal fin with iii or iv unbranched rays, 8–9 branched rays, anterior margin straight, posterior margin slightly concave. Position of pelvic-fin origin not settled, anterior, vertical, or posterior to posterior end of dorsal-fin base. Pelvic fin with i,5 rays; tip of adpressed fin beyond anus, rarely reaching anal-fin origin. Pectoral fin with I,11, I,12, I,13 rays; posterior margin slightly concave. Pectoral-fin spine with filamentous extensions comparatively short, reaching anterior pelvic-fin base. Spine with smooth anterior margins and serrated posterior margins.

Coloration. In 75% ethanol: dorsal and ventral surfaces of head and body gray, ventral surfaces light yellow. Long-term preserved specimens dark yellow overall. Three dark brown saddles below dorsal fin, below adipose fin, and on posterior half of caudal peduncle extending to base of caudal fin, respectively. Dorsal fin ash gray, dorsal-fin base brown. Pectoral fins gray with light posterior margins. Pelvic fin gray with an inconspicuous brown band. Anal fin ash gray, with brown base and a brown

Table 2. Morphometric data for *Bagarius protos* sp. nov. and *Bagarius dolichonema* sp. nov.

	***Bagarius protos* sp. nov.(n = 13)**			***Bagarius dolichonema* sp. nov.(n = 21)**		
	Holotype	**Range**	**Mean ± SD**	**Holotype**	**Range**	**Mean ± SD**
Standard length (mm)	319.0	261.2–434.0		216.6	128.7–252.7	
% of SL						
Predorsal length	34.9	33.0–41.8	38.5 ± 2.5	38.7	36.4–39.8	38.7 ± 0.9
Preanal length	70.4	67.6–75.7	70.1 ± 2.1	69.7	67.2–73.3	69.6 ± 1.3
Prepelvic length	52.1	47.3–52.2	49.4 ± 1.7	49.4	48.2–52.8	50.3 ± 1.3
Prepectoral length	27.4	22.8–28.2	25.9 ± 1.7	25.3	22.5–27.3	25.4 ± 1.2
Length of dorsal-fin base	14.0	9.8–15.4	12.7 ± 1.4	11.7	10.6–12.4	11.4 ± 0.7
Dorsal-fin spine length	15.7	13.9–17.5	15.5 ± 1.1	13.2	12.4–17.3	14.5 ± 1.6
Length of anal-fin base	13.4	11.9–14.6	12.9 ± 0.7	13.3	11.4–14.3	13.0 ± 0.7
Pelvic-fin length	20.0	15.8–20.1	18.7 ± 1.2	15.6	14.7–17.7	15.9 ± 0.9
Pectoral-fin length	31.1	29.0–37.7	32.8 ± 2.7	27.9	23.8–38.1	30.2 ± 4.2
Pectoral-fin spine length	15.9	12.2–18.6	15.4 ± 1.7	14.2	13.4–16.7	14.9 ± 0.9
Caudal-fin length	28.9	24.7–43.4	30.1 ± 4.8	34.2	25.6–62.5	42.8 ± 10.8
Length of adipose-fin base	14.8	12.6–14.8	13.4 ± 0.6	13.6	10.1–14.0	12.7 ± 1.1
Dorsal to adipose distance	21.6	19.5–22.9	20.8 ± 1.0	22.7	19.7–25.4	22.2 ± 1.2
Post-adipose distance	16.4	15.2–18.0	16.3 ± 0.9	15.5	15.5–18.8	17.0 ± 1.0
Length of caudal peduncle	17.5	16.6–18.7	17.5 ± 0.6	16.3	16.3–20.4	17.6 ± 1.2
Depth of caudal peduncle	4.6	4.2–5.1	4.8 ± 0.3	4.1	3.8–4.6	4.2 ± 0.2
Body depth at anus	13.5	11.7–15.6	13.3 ± 1.0	10.8	10.0–14.7	11.3 ± 1.2
Head length	31.4	30.3–32.8	31.5 ± 0.6	31.4	30.1–34.0	31.9 ± 0.9
Head width	25.6	21.8–25.6	24.0 ± 1.3	22.2	21.1–25.4	22.8 ± 1.2
Head depth	15.4	12.9–17.6	15.2 ± 1.4	16.7	13.0–17.6	15.1 ± 1.2
% of head length						
Snout length	53.5	49–55	52 ± 1.8	48	48–54	50 ± 1.7
Interorbital distance	30	26–31	28 ± 1.5	25	25–32	28 ± 1.7
Eye diameter	7	5–8	6 ± 0.7	9	6–11	8 ± 1.2
Nasal barbel length	5	5–7	6 ± 0.8	3	2–6	4 ± 1.0
Maxillary barbel length	92	76–103	93 ± 6.5	79	73–95	83 ± 5.6
Inner mandibular barbel length	22	15–23	20 ± 2.1	18	16–23	18 ± 1.8
Outer mandibular barbel length	34	26–38	32 ± 3.4	29	25–33	29 ± 2.1

Figure 2. Living specimens of *Bagarius protos* sp. nov., paratype. KIZ202410548, 324 mm SL.

band. Caudal fin light gray. Head, body, and each fin with irregularly scattered small dark spots. The gray parts in 75% ethanol show grayish yellow when alive.

Etymology. The epithet name "*protos*" consists of the Greek "protos," meaning original (at first), referring to the species being in the most primitive position in the

Figure 3. Habitat of *Bagarius protos*, Bizhai Township, Longling County, Yunnan Province. Photo by Shu-Sen Shu.

phylogenetic tree of genus *Bagarius*. The suggested common name in Chinese is 原鮀 (Pinyin: yuan pi).

Distribution and ecology. The new species is distributed in the mainstream of the Nujiang River and the Nanting River in China (Figs 3, 8), also expected to occur on the Salween River in Myanmar and Thailand.

Notes on habits. *Bagarius protos* used to be a local high-value food fish that lived in the mainstream of the Nujiang River. According to the locals, it can grow to over 100 kg. Local people used to catch *B. protos* by longline fishing, using Corydalidae larva or loach as bait and thick nylon rope as a line, tying one end to a boulder, and harvesting it on the next day. Even large individuals of *B. protos* over 10 kg are still attracted by Corydalidae larvae, showing the preference of *B. protos* for this prey.

Bagarius dolichonema Zeng & Chen, sp. nov.

https://zoobank.org/921C49DF-C401-41F6-9418-6602A2B442F1

Figs 4, 5, Table 2

Bagarius sp. 'Irrawaddy' Ng & Kottelat, 2021: 141 (Irrawaddy River).

Type material. ***Holotype.*** • KIZ2024010545, 216.6 mm SL, Min Sin, Downstream of Nam E Zu, a tributary of the Chindwin River, Sagaing Province, Myanmar, 25°31'20.7"N, 95°29'44.2"E, leg. Tao Qin, Nay Htet Naing, May 2019.

Paratypes. • KIZ2024010547, S20191939-1940, 3 ex, 135.5–177 mm SL, fish market of Hta Man Thi village, Chindwin River, Sagaing Province, Myanmar, 25°20'01.8"N, 95°17'12.4"E, leg. Tao Qin, Nay Htet Naing, Lamin Koko, December 2019; • KIZ2024010543, 1 ex, 251.3 mm SL, Kalaywa market, Chindwin River, Sagaing Province, Myanmar, 23°11'47.3"N, 94°17'49.8"E, leg. Paing Zaw, Nay Htet Naing, March 2018; S20180428, • KIZ2024010544, 2 ex, 150.6–226.5 mm SL, Hkamti market, Chindwin River, Sagaing Province, Myanmar, 26°00'06.4"N, 95°41'32.4"E, leg. Paing Zaw, Nay Htet Naing, May 2018; • KIZ2024010542, CXY20170154, 2 ex, 193.9–198.3 mm SL, Fish market of Pyay, Irrawaddy River, Bago Province, Myanmar, 18°50'06.1"N, 95°13'12.0"E, leg. Xiao-Yong Chen, Tao Qin, Shu-Sen Shu, Paing Zaw, Ye Yint Tun, Nay Htet Naing, June 2017; • KIZ2024010546, 1 ex, 128.7 mm SL, Stream of Nam Pagon, a tributary of the Chindwin River, Sagaing Province, Myanmar, 25°18'45.2"N, 95°31'40.9"E, leg. Tao Qin, Nay Htet Naing, Lamin Koko, December 2019; • KIZ2007004082-083, • KIZ2007004088, 3 ex, 206.4–252.7 mm SL, Kalay fish market, Myittha River, Sagaing Province, Myanmar, 23°10'53.1"N, 94°05'24.1"E, leg. De-Xin Feng, August 2007.

Diagnosis. *Bagarius dolichonema* can be distinguished from congeners by the following combination of characteristics: lateral margin of frontal straight, not forming brow ridge, dorsal spine strong (width 9.9–14.1 times its length), weakly notched antero-dorsal margin on pterygiophore of first dorsal-fin, filamentous extensions of pectoral-fin spine beyond posterior of pelvic-fin base and some reaching anus, neural spines of 4th–6th vertebrae immediately anterior to adipose fin distally slightly flattened, adipose-fin origin at vertical through or very slightly posterior to anal-fin origin, caudal peduncle slender (3.8–4.6% SL).

Description. Head depressed; body subcylindrical, becoming more laterally compressed at caudal peduncle. Dorsal profile rising evenly from tip of snout to origin of dorsal fin, then sloping gently ventrally from origin of dorsal fin to end of caudal peduncle. Ventral profile straight to anal-fin base, then sloping gently dorsally from anal-fin base to end of caudal peduncle. Anus and urogenital openings located approximately 1/2 to 2/3 distance between base of last pelvic-fin ray and base of first anal-fin ray. Skin tuberculated, with tubercles of varying sizes on sides of body; larger tubercles arranged in longitudinal rows along dorsal head and dorsal lateral surfaces of body. Lateral line complete and situated mid-laterally. Vertebrae 21+20=41*(4).

Head depressed and broad, triangular when viewed laterally. Snout prominent. Anterior and posterior nares adjacent, separated by base of nasal barbel. Gill opening broad, extending from ventral margin of post-temporal to isthmus. Dorsal surface of head covered by thick skin and ovoid tubercles. Eye small and ovoid; lateral margin of frontal not forming brow ridge. Base of supraoccipital spine wide, occipital bone triangular.

Barbels in four pairs. Maxillary barbel subtended by large skin flap along posterior edge of proximal half of barbel connected with side of snout; extending to middle of pectoral-fin base. Nasal barbel short, just extending to posterior margin of posterior nares. Outer mandibular barbel extending to vertical line through eye. Inner mandibular barbel about 2/3 of outer mandibular barbel in length.

Mouth inferior, most anterior part of premaxillary tooth band exposed when mouth closed. Oral teeth cone-shaped, varying in size, and irregularly aligned on all tooth-bearing surfaces. Premaxillary teeth form a broad semilunar band, interrupted at midline.

Dorsal fin located above anterior one-third of body, with I,6 rays; dorsal spine straight and strong, smooth both on anterior and posterior margins, width 9.9–14.1

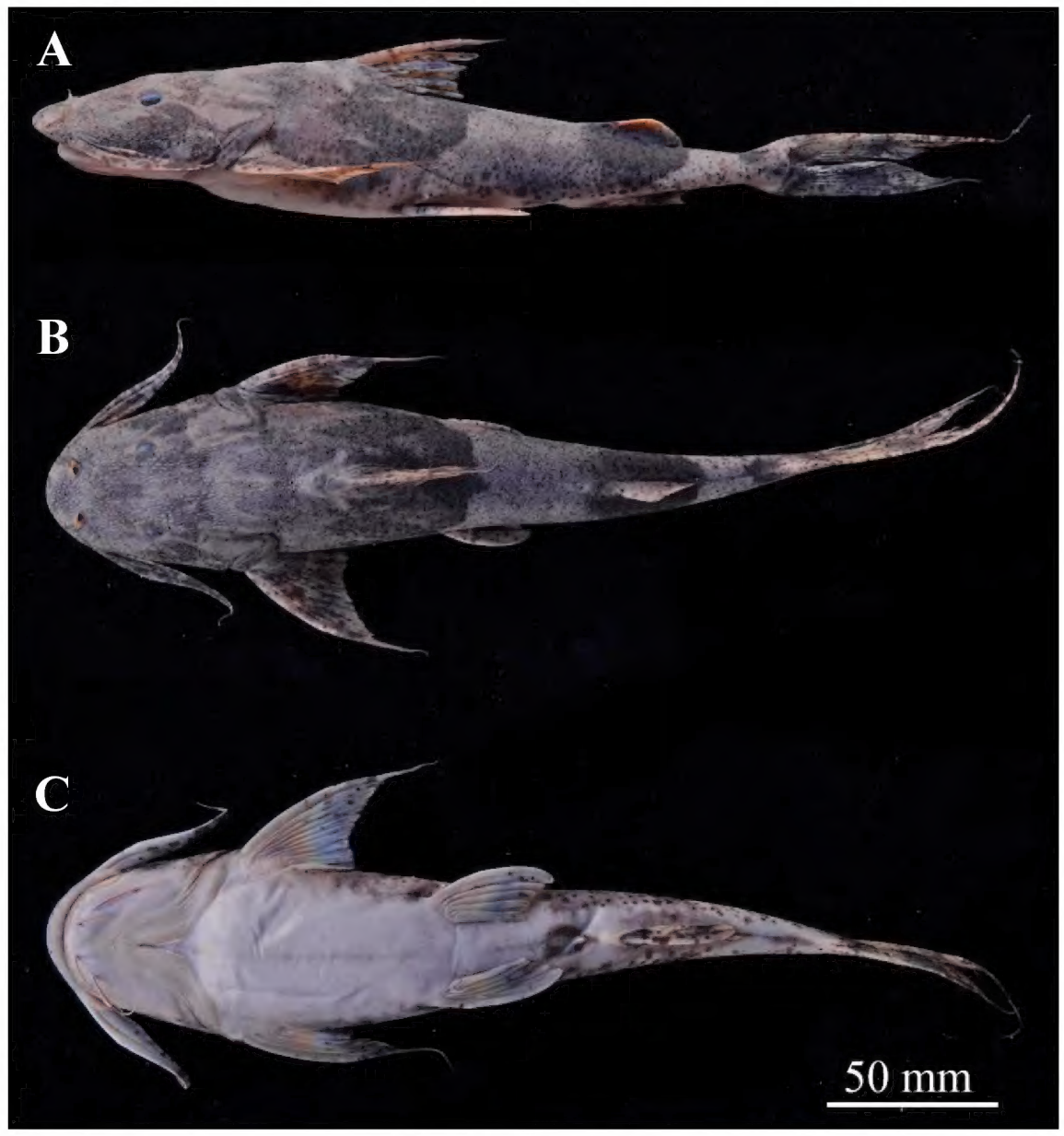

Figure 4. Lateral (**A**), dorsal (**B**), and ventral (**C**) views of *Bagarius dolichonema* sp. nov., KIZ2024010545, holotype, 216.6 mm SL.

Figure 5. Fresh specimens of *Bagarius dolichonema* sp. nov., paratype, KIZ2024010542, 193.9 mm SL, photo by Tao Qin.

times its length. Adipose fin triangular, with anterior margin straight or slightly concave. Adipose fin origin at vertical through or very slightly posterior to anal-fin origin. Caudal fin rays i,7,7,i or i,7,8,i, strongly forked, with upper lobe longer than lower lobe and principal rays. Filamentous extensions with caudal fin extremely extending. Anal fin with straight anterior margin and concave posterior margin; with unbranched ray iii, branched ray 8, 9, or 10 rays. Pelvic-fin origin at vertical through posterior end of dorsal-fin base. Pelvic fin with slightly convex margin and i,5 rays; tip of pelvic fin usually not reaching anal-fin origin, rarely reaching. Pectoral fin with I,10, I,11, I,12, I,13 rays; posterior margin slightly concave. Pectoral-fin spine with filamentous extension beyond anterior pelvic-fin base, or even reaching anus, smooth on anterior margin, serrated on posterior margin.

Coloration. In 75% ethanol: dorsal and ventral surfaces of head and body dark gray, ventral surface pale. Three dark brown saddles below dorsal fin, below adipose fin, and in posterior one-third of caudal peduncle.

Figure 6. Habitat of *Bagarius dolichonema*, Min Sin, Downstream of Nam E Zu, a tributary of the Chindwin River, Sagaing Province, Myanmar. Photo by Tao Qin.

Dorsal fin dark gray with a medium brown band. Pectoral and pelvic fins dark gray. Anal fin gray with a dark patch close to its origin and a dark brown band in posterior part. Caudal fin gray, with dark patches at caudal-fin base, middle of upper and lower lobes. Head, body, and each fin with small dark spots, density of spots variable, absent in some individuals. Body more brown when alive.

Etymology. The epithet name "*dolichonema*" comes from the Greek adjective "dolikhos," meaning long, and the noun "nēma," meaning thread or yarn, which refers to the length of filamentous extensions with pectoral-fin spines and caudal fins that are the longest in congeners except for *B. bagarius*. The suggested common name in Chinese is 长丝鮀 (Pinyin: chang si pi).

Figure 7. Gastric contents of *B. dolichonema* from (**A**) KIZ2007004088 and (**B**) KIZ2007004083. Images not to scale.

Distribution. Known to be found in the Irrawaddy River Basin in Myanmar (Figs 6, 8) and the Manipur River in India, with its presence also expected in the Chinese part of the Irrawaddy River Basin.

Notes on habits. *B. dolichonema* is also caught and sold as a food fish in Myanmar. In 2007, considerable quantities of *B. dolichonema* were sold on the Kalay fish market. In the stomachs of two specimens of *B. dolichonema* that were purchased, shrimp and crab pincers were found in one, and *Glyptothorax nagpang* with half-digested Cyprinidae fish was found in the other Fig. 7. This reveals the broader diet of *B. dolichonema*, which is capable of feeding on prey in a variety of environments and swallowing parts of its body even when the prey is too large (e.g., crabs). *B. dolichonema* is still receptive to prey with sharp spines and swallows them into its stomach for digestion.

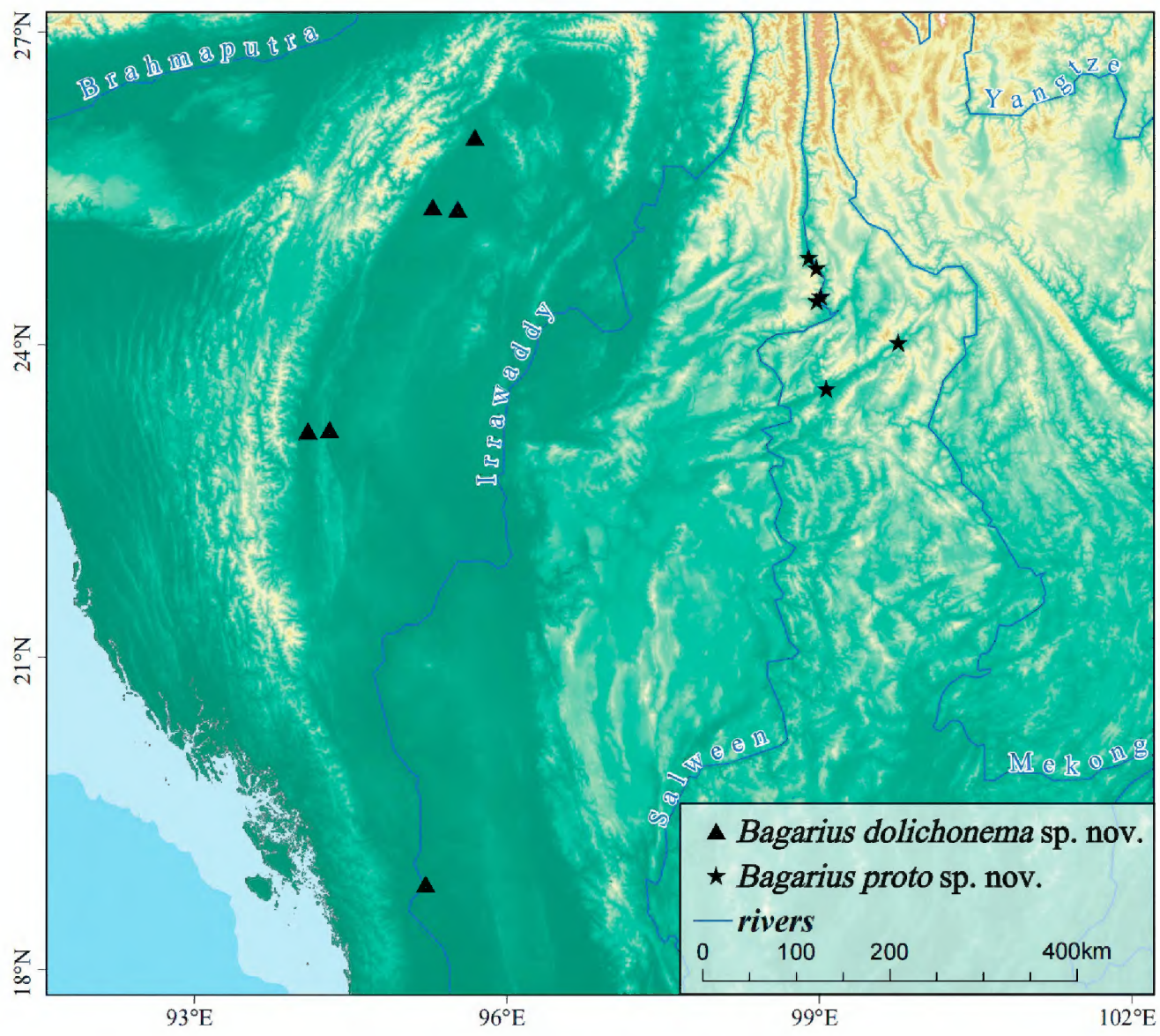

Figure 8. Map showing collection localities of *Bagarius protos* and *B. dolichonema*.

Molecular analysis

A total of 660 bp were included in the aligned dataset of the *CO*I gene, comprising 512 conserved sites, 148 variable sites, 132 parsimony-informative sites, and 16 singleton sites. The phylogenetic trees reconstructed using ML and BI methods are largely congruent in topology (Fig. 9). The validity of *Bagarius protos* sp. nov. and *B. dolichonema* sp. nov. is strongly supported by the molecular phylogenetic results. *B. protos* is located at the base of the *Bagarius* phylogeny, and *B. dolichonema* is the sister group of *B. bagarius*. The BI tree shows that *B. lica*, *B. rutilus*, and *B. vegrandis* are all monophyletic, but their phylogenetic relationships are not clearly resolved. A clearer phylogenetic pattern is shown by the ML tree, although with weak support. This may indicate relatively close relationships among these taxa.

The estimated K2P genetic distances of the *CO*I gene within *Bagarius* are shown in Table 3. The distances between *B. protos* and its congeners range from 8.0% to 12.6%, and the distances between *B. dolichonema* and its congeners range from 5.7% to 12.1%, Table 3.

Table 3. K2P distances (%) for species within genus *Bagarius*, based on the *CO*I gene, the minimum distances between multiple samples are shown.

	1	2	3	4	5	6
1. *B. protos*						
2. *B. dolichonema*	8.8					
3. *B. bagarius*	9.8	5.7				
4. *B. lica*	8.1	8.8	8.5			
5. *B. rutilus*	8.0	8.4	9.4	2.1		
6. *B. vegrandis*	11.1	11.0	12.8	6.2	6.0	
7. *B. suchus*	12.6	12.1	12.2	9.0	9.4	10.5

Discussion

The first species of *Bagarius*, *Pimelodus bagarius*, was described by Hamilton (1822) and later reassigned to the genus *Bagarius* by Bleeker (1853). Roberts (1983) described *B. suchus* from the Mekong and Chao Phraya rivers in Thailand and Laos. He resurrected *B. yarrelli* (Sykes, 1839) from synonymy with *B. bagarius*, believing it to be widespread in South and Southeast Asia. He also redefined *B. bagarius* as a small-sized species restricted to the Ganges, Mekong, and Chao Phraya rivers. In addition, Roberts recognized specimens of *Bagarius* from the Red River and Nam Ma drainages as a distinct species, later described as *B. rutilus* by Ng and Kottelat (2000).

Ng and Kottelat (2021) reexamined *Bagarius* specimens from South and Southeast Asia and made a major taxonomic revision. *Bagarius bagarius* (Hamilton, 1822) was shown to be a species restricted to the Indian subcontinent, with *B. yarrelli* treated as its junior subjective synonym. *Bagarius lica* Volz, 1903, was resurrected from synonymy with *B. yarrelli* as a valid species occurring from the Mekong drainage to the Dong Nai River drainage (China, Laos, Thailand, Cambodia, and Vietnam), extending southwards to Malaysia, Sumatra, Borneo, and Java in Southeast Asia. *Bagarius vegrandis*, a small-sized species, was described from the Chao Phraya and Mekong River drainages. The specimens they examined from the Irrawaddy and Salween River drainages, temporarily referred to as *Bagarius* sp. 'Irrawaddy' and *B.* sp. 'Salween,' correspond to *B. dolichonema* and *B. protos*, respectively, in this study.

Bagarius protos differs from *B. lica* in having a straight lateral margin of the frontal, which is not significantly deflected dorsally to form a brow ridge (vs. significantly deflected dorsally to form a brow ridge; Fig. 10). It differs from *B. rutilus* in having dark yellow fins in life (vs. orange fins in life). *B. protos* is

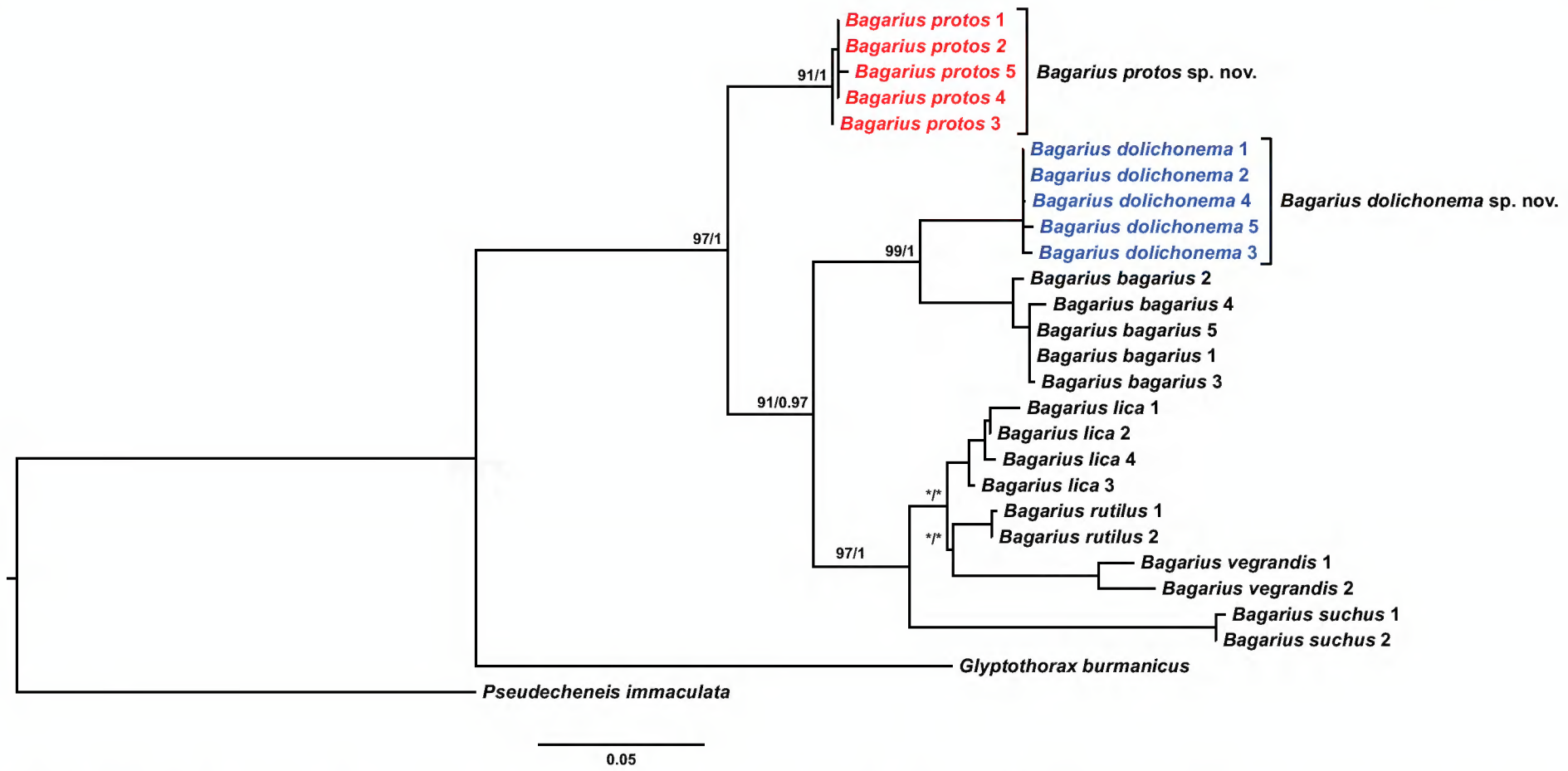

Figure 9. Bayesian inference tree and maximum likelihood tree of genus *Bagarius* inferred from *CO*I gene sequences. Bayesian posterior probabilities (> 0.8) and Maximum Likelihood bootstrap values (> 70%) are shown.

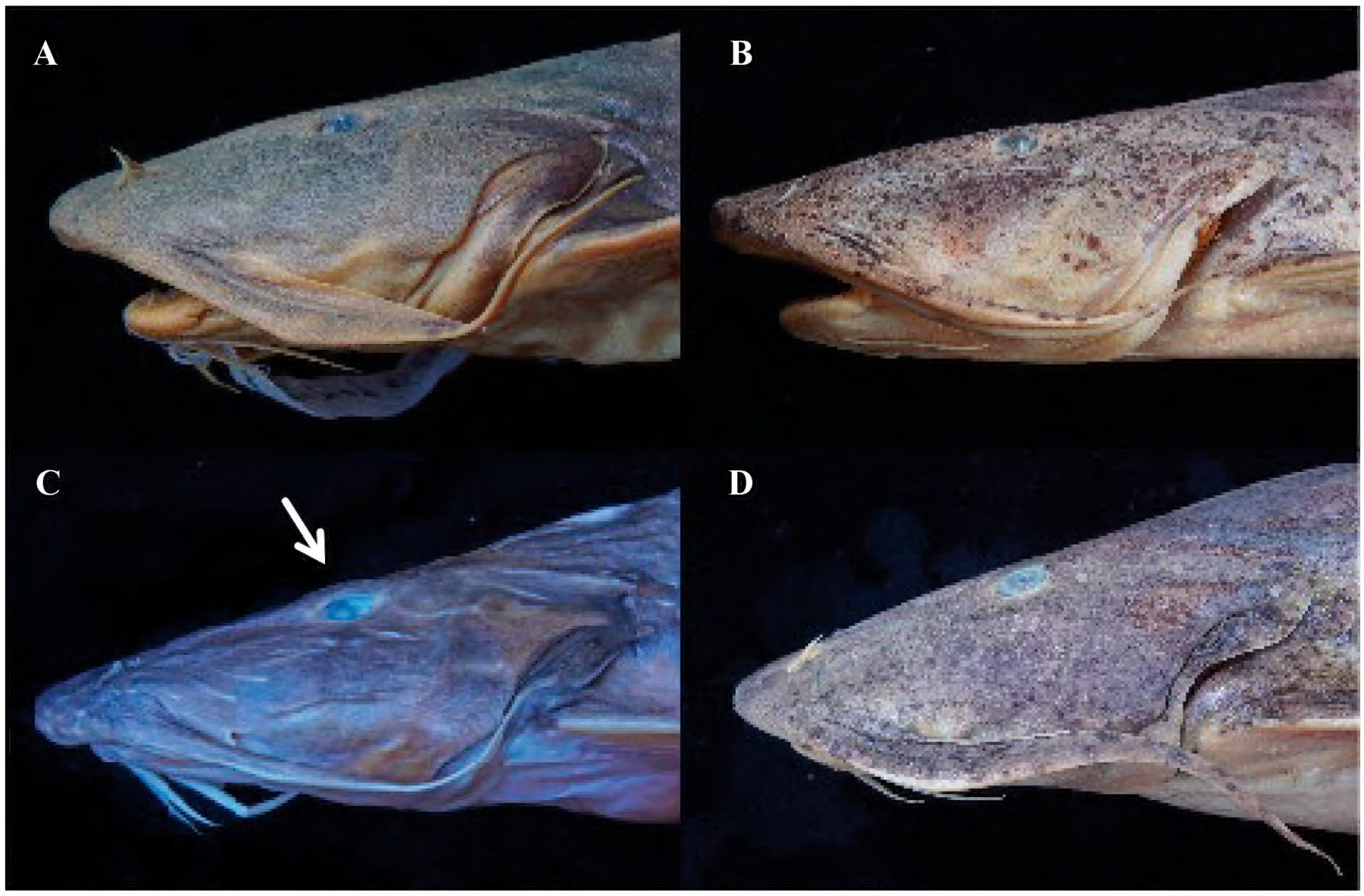

Figure 10. Lateral views of heads of: **A.** *Bagarius protos*, KIZ2004015368, 261.2 mm SL; **B.** *B. dolichonema*, KIZ2007004082, 252.7 mm SL; **C.** *B. lica*, KIZ202400840, 275.0 mm SL; **D.** *B. vegrandis*, KIZ2010001566, 276.8 mm SL. Arrow indicates dorsally deflected lateral margin of frontal forming brow ridge over orbit. Images not to scale.

distinguished from *B. dolichonema* by a strongly (vs. weakly) notched anterodorsal margin of the first dorsal-fin pterygiophore (Fig. 11), a greater number of total vertebrae (43 vs. 41), shorter filamentous extensions of the pectoral-fin spine (just reaching posterior of pelvic-fin base vs. extending beyond the pelvic-fin base, some reaching the anus), and distally slender (vs. slightly flattened) neural spines of vertebrae 4th–6th immediately anterior to the adipose fin (Fig. 12). *Bagarius protos* differs from *B. bagarius*, *B. vegrandis*, and *B. suchus* in having smaller eyes (5–8% HL vs. 9–12% HL for *B. bagarius*, 8–15% HL for *B.vegrandis*, and 9–10% HL for *B. suchus*) and a deeper caudal peduncle (4.2–5.1% SL vs. 3.5–4.1% SL for *B. bagarius*, 3.2–4.2% SL for *B. vegrandis*, and 3.2–3.4% SL for *B. suchus*). It further differs from *B. suchus* and *B. vegrandis* in its larger known maximum size (up to 1,000 mm SL vs. 281 mm SL for *B. vegrandis* and 520 mm SL for *B. suchus*), distally slender (vs. flattened) neural spines of vertebrae 4th–6th immediately anterior to the adipose fin, and the adipose-fin origin nearly at vertical through to (vs. markedly posterior to) the anal-fin origin. *Bagarius protos* also differs from *B. suchus* in having a deeper head (12.9–17.6% SL vs. 6.8–8.5% SL) and body (depth at anus 11.9–15.6% SL vs. 7.6–8.1% SL). It differs from *B. vegrandis* in having more preanal vertebrae (23 vs. 19–20) and more total vertebrae (43 vs. 39–40). Additionally, it differs from *B. bagarius* in having shorter filamentous extensions of the pectoral-fin spine (just reaching the posterior of the pelvic-fin base vs. extending posterior to the anus), a strongly (vs. weakly) notched anterodorsal margin of the first dorsal-fin pterygiophore, and a stronger dorsal spine (width 10.6–14.4 times its length vs. 13.5–19.4).

Bagarius dolichonema differs from *B. bagarius* in having a stronger dorsal spine (width 9.9–14.1 times its length vs. 13.5–19.4), shorter filamentous extension of the pectoral spine (extending beyond posterior of pelvic-fin base, some reaching anus vs. reaching posterior to anus), and neural spines of the 4th–6th vertebrae immediately anterior to the adipose fin distally slightly flattened (vs. slender). It differs from *B. lica* and *B. rutilus* in having a weakly (vs. strongly) notched antero-dorsal margin of the first pterygiophore of the dorsal fin, fewer preanal vertebrae (22 vs. 23–24) and total vertebrae (41 vs. 43–44 in *B. lica*, 42–42 in *B. rutilus*), longer filamentous extension of the pectoral-fin spine (extending beyond posterior of pelvic-fin base, some reaching anus vs. just reaching posterior of pelvic-fin base), and distally slightly flattened (vs. slender) neural spines of the 4th–6th vertebrae immediately anterior to the adipose fin. It further differs from *B. lica* in the lateral margin of the frontal not significantly deflected dorsally to form a brow ridge (vs. significantly deflected dorsally to form a brow ridge) and in having a more slender caudal peduncle (depth 3.8–4.6% SL vs. 4.5–5.2% SL). It differs from *B. suchus* and *B. vegrandis* in having a larger known maximum size (to 1,000 mm SL vs. to 281 mm SL in *B. vegrandis* and 520 mm SL in *B. suchus*), distally slightly flattened (vs. flattened) neural spines of the 4th–6th vertebrae immediately anterior to the

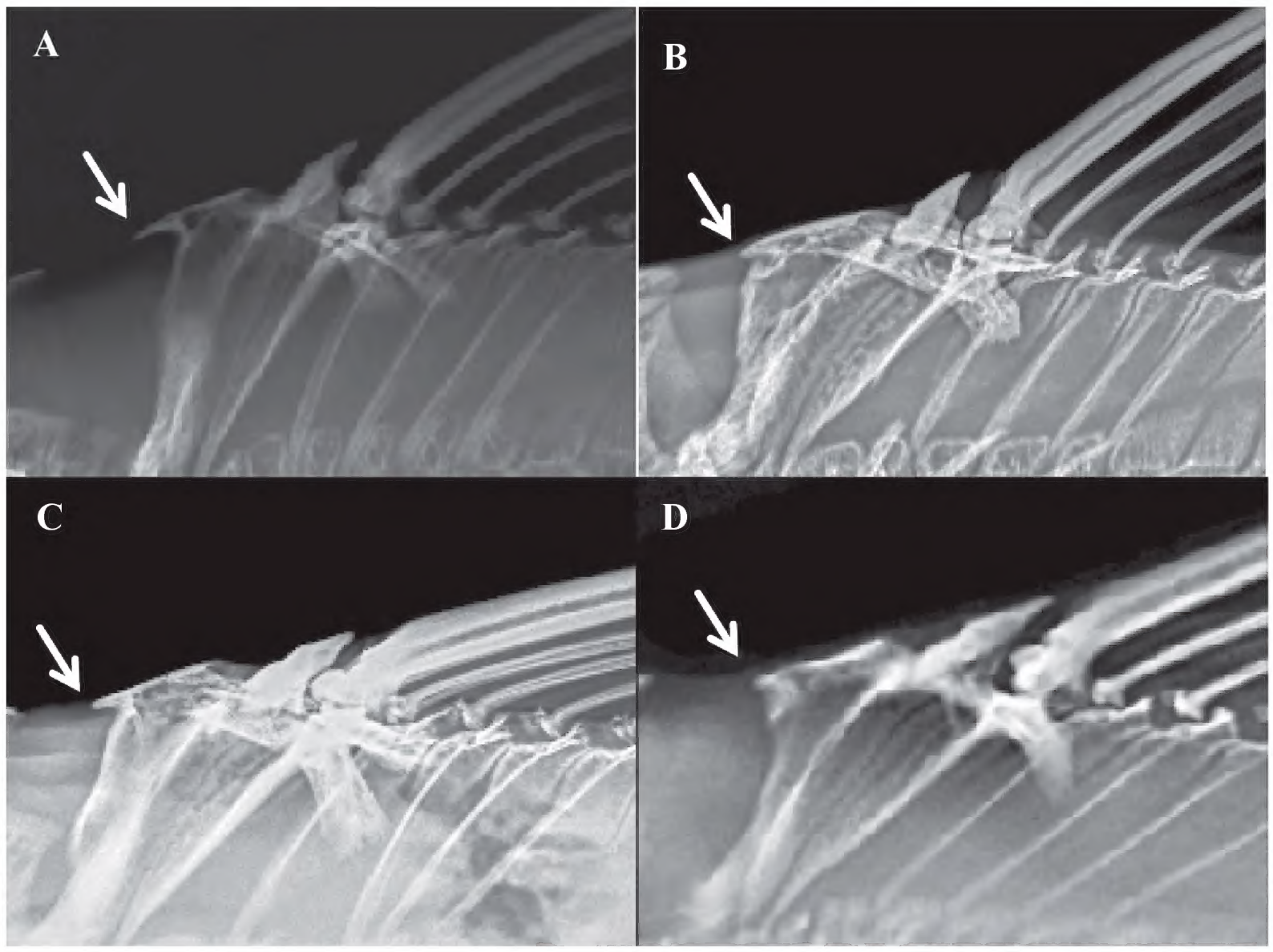

Figure 11. Lateral views of first dorsal pterygiophore on a radiograph of: **A.** *Bagarius protos*, KIZ2004015368, 261.2 mm SL; **B.** *B. dolichonema*, KIZ2007004082, 223.9 mm SL; **C.** *B. lica*, KIZ202400840, 275 mm SL; **D.** *B. bagarius*, UMMZ 244958, 153.4 mm SL (from Ng and Kottelat 2021). Images not to scale.

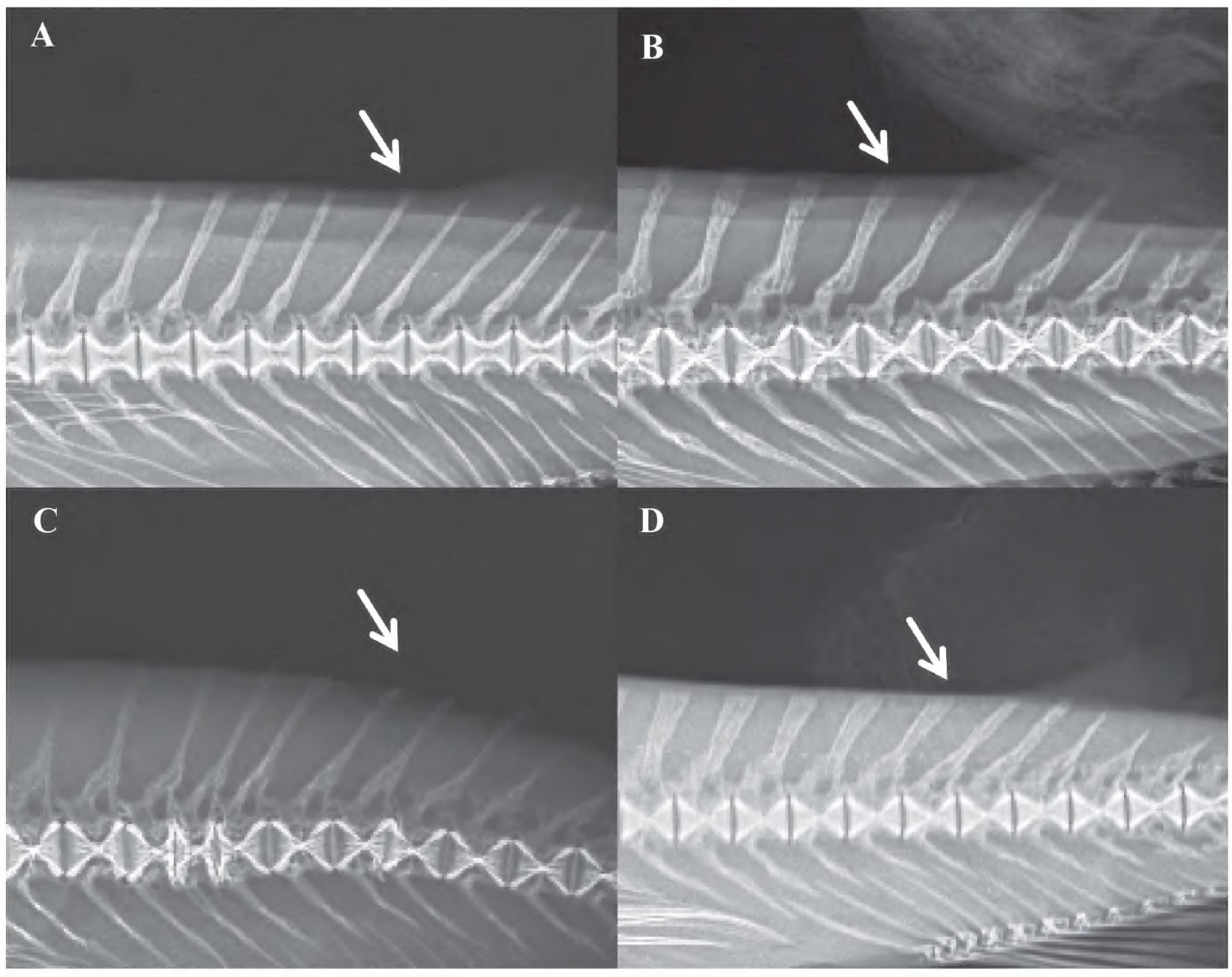

Figure 12. Lateral views of neural spines of the 4th–6th vertebrae immediately anterior to the adipose fin under x-ray of: **A.** *Bagarius protos*, KIZ2004015368, 261.2 mm SL; **B.** *B. dolichonema*, KIZ2007004082, 223.9 mm SL; **C.** *B. lica*, KIZ202400840, 275 mm SL; **D.** *B. vegrandis*, KIZ2024010000, 190 mm SL. Images not to scale.

adipose fin, the adipose-fin origin nearly vertical through to (vs. markedly posterior to) the anal-fin origin, and a strongly (vs. weakly) notched antero-dorsal margin of the first dorsal-fin pterygiophore. The species further differs from *B. vegrandis* in having more preanal vertebrae (22 vs. 19–20). It differs from *B. suchus* in having a deeper head (13.0–17.6% SL vs. 6.8–8.5% SL), a deeper body (depth at anus 10.0–14.7% SL vs. 7.6–8.1% SL), and a deeper caudal peduncle (3.8–4.6% SL vs. 3.2–3.4% SL).

Key to species of *Bagarius*

1 Adipose-fin origin markedly posterior to the anal-fin origin 2
– Adipose-fin origin nearly at vertical through to the anal-fin origin 3
2 Head and body deep, head depth 11.1–14.1% SL, depth at anus 8.7–12.0% SL (Chao Phraya River drainages in Thailand and Mekong River drainages in China, Laos, Thailand, and Cambodia, with its presence also expected in Vietnam) ... *B. vegrandis*
– Head and body slender, head depth 6.8–8.5% SL, depth at anus 7.6–8.1% SL (Chao Phraya and Mekong River drainages in Thailand and Laos) ..... *B. suchus*
3 Filamentous extension of the pectoral spine beyond end posterior of pelvic fin base, antero-dorsal margin of the first dorsal pterygiophore weakly notched 4
– Filamentous extensions of the pectoral-fin spine just reaching end posterior of pelvic fin base, anterodorsal margin of the first dorsal pterygiophores strongly notched 5
4 Dorsal spine strong, width 9.9–14.1 times its length, neural spines of the 4th–6th vertebrae immediately anterior to the adipose fin distally slightly flattened (Irrawaddy River drainages in Myanmar and India, with its presence also expected in China) ..... *B. dolichonema*
– Dorsal spine narrow, width 13.5–19.4 times its length, neural spines of the 4th–6th vertebrae immediately anterior to the adipose fin distally slender (Indian subcontinent, including Pakistan, India, Nepal, Bhutan, Bangladesh, and the southern Xizang region of China) ..... *B. bagarius*
5 Fins orange in life (Red River drainages in China and Vietnam, Nam Ma drainages in Laos and Vietnam) ..... *B. rutilus*
– Fins dark yellow in life 6
6 The lateral margin of the frontal significantly deflected dorsally to form a brow ridge (Mekong River drainage to the Dong Nai River drainages in China, Thailand, Laos, Cambodia, and Vietnam and southwards to Malaysia, Sumatra, Borneo, and Java) ..... *B. lica*
– The lateral margin of the frontal not significantly deflected dorsally to form a brow ridge (Nujiang River [Salween River] drainages in China, also expected to occur on the Salween River drainages in Myanmar and Thailand) ..... *B. protos*

Comparative materials examined

1. *Bagarius lica*: KIZ1996002687-688, 284.5–430 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County: Menglun Town, Luosuojiang River; KIZ2002031201, 397 mm SL, China: Yunnan Province: Lincang City: Yun County: Dachaoshan, Langcangjiang River; KIZ1973001215-222, 92.5–271.9 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Jinghong City: Menghan County: Langcangjiang River; KIZ2001003736, 184.4 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Jinghong City: Ganlanba, Langcangjiang River; KIZ2004014942-943, 132.2–166.1 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County: Menglun Town, Luosuojiang River; YNAU20230701L01, 662 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Jinghong City: Menghan County: Langcangjiang River; KIZ2024000840, 269.7 mm SL, China: Yunnan Province: Puer City: Cuiyun District: Nuozhadu, Langcangjiang River; KIZ2012001261, 163.1 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County: Menglun Town, fish market.
2. *Bagarius vegrandis*: KIZ2014000662, 179.3 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County: Menglun Town, Luosuojiang River; KIZ2010001566, 281.0 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County: Menglun Town, Luosuojiang River; KIZ2012001583, 173.6 mm SL, China: Yunnan Province: Puer City: Cuiyun District: Nuozhadu, Nandianhe River; KIZ2012001263-264, 137.4–153.9 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County: Menglun Town, fish market; KIZ1996002798, 133.4 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Jinghong City: Langcangjiang River; KIZ2014004356, 266.0 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County: Menglun Town, Luosuojiang River; KIZ2024010000, 224.4 mm SL, China: Yunnan Province: Xishuangbanna Dai Autonomous Prefecture: Mengla County: Guanlei Town, Nanlahe River.

3. *Bagarius bagarius*: KIZ2024010551-553, 131.0–184.6 mm SL, India: Assam State: Dibrugarh district: Jamuna River.
4. *Bagarius rutilus*: KIZ1992000238, 399 mm SL, Vietnam: Lào Cai Province: Lào Cai City: Red River; KIZ2003005723, 311 mm SL, China: Yunnan Province: Honghe Hani and Yi Autonomous Prefecture: Luchun County: Lixianjiang River; KIZ1975000182-183, 151.9–153.7 mm SL, China: Yunnan Province: Wenshan Zhuang and Miao Autonomous Prefecture: Malipo County, Panlonghe River; KIZ2023000063, 158.7 mm SL, China: Honghe Hani and Yi Autonomous Prefecture: Yuanyang County: Nansha Town: Yuanjiang River; KIZ2024010549, 196.2 mm SL, China: Honghe Hani and Yi Autonomous Prefecture: Yuanyang County: Nansha Town: Yuanjiang River.
5. *Bagarius suchus*: KIZ2024001049, 234.5 mm SL, probably collected in Thailand, purchased from Huadiwan Flower and Bird Market, Guangzhou, China; KIZ2024010550, 276.5 mm SL, probably collected in Thailand, purchased from Huadiwan Flower and Bird Market, Guangzhou, China.

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Authors' contributions

Yu-Yang Zeng conducted specimen collection, identification, and examination; extracted DNA; photography and cartography; molecular genetic analysis; and manuscript preparation. Xin-Rui Pu handled specimen measurements and calculation of morphological data. Hao-Tian Lei provided part of the specimens and revised the manuscript. Thaung Naing Oo provided assistance in the conduct of fieldwork and collection of specimens. Xiao-Yong Chen designed the study, provided guidance on this research, and reviewed and revised the manuscript. All authors read and approved the final version of the manuscript.

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